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ON THE

DEVELOPMENT OF THE EXTERNAL EAR PASSAGES.

By DAVID HUNT, M. D.,

OF BOSTON, MASS.

The history of embryology contained but little of interest, as far as the development of the ear was concerned, until von Baer published his classical observations in 1828. In the seventeenth century a number of the most excellent observers busied themselves with the anatomy of the ear, and at the same time were more or less engaged in those studies of development which have made the century an epoch in the history of embryological research; still we miss anything like an earnest attempt to account for the origin of the intricate parts contained in the organ of hearing.

Early in the present century von Baer and Huschke may be said to have placed the study of the development of the ear upon a solid basis. The plan of their work is still good, and as far as the meatus and Eustachian tube is concerned, the details have scarcely been added to.

It so happened that the formation of the ear became a subject of controversy between von Baer and Huschke; the former, misled by the seeming analogy between the otic and optic vesicles, described the ear as an offshoot from the brain.[1]

Huschke attacked this view,[2] and proved that the otic vesicle is an involution of the tegumentary layer of the embryo. At the same time von Baer stated an opinion as to the development of the meatus and Eustachian tube[3] that was opposed by Huschke; here also the latter has been declared the victor, but I believe incorrectly.

Huschke's[4] views now prevail, and have been supported by Valentin,[5] Rathke,[6] and Bischoff.[7]

[1] Ueber Entwickelungsgeschichte der Thiere Königsburg, 1828; Easter Thiel, p. 30.

[2] Isis von Oken, 1831, heft. 8–10, seite 951.

[3] Op. citat., Part I. pp. 77, 106, 122, 131, and Part II. p. 116.

[4] Op. citat., vol. xx. p. 401, 1828; p. 162, 1828; p. 951, 1831; Merkel's Archiv für Anatomie und Physiologie, 1832, p. 40.

[5] Lehrbuch der Physologie des Menschen, Braumschweig, 1847.

[6] Anat. Physiol. Untersuchungen über den Kiemenapparat, 1832, pp. 119 and 120.

[7] Entwickelungsgeschichte des Hunde Eies. Braumschweig, 1845, p. 109.

As evidence of the confusion which exists on the subject, it may be stated that Kölliker, in the new edition of his *Entwickelungsgeschichte des Menschen und der hoheren Thiere* (Leipzig, 1876), describes the first cleft as closed in an embryo of ten days (p. 300) and open in another at the same age (p. 253), and Mr. W. K. Parker[1] describes the cavity of the auditory vesicle as the first branchial cleft.

One cause of the confusion which has heretofore existed, in the description of the mode of closure of the first branchial cleft, has been that the stages of development of the embryos under examination have been too far apart; another frequent cause has been the advanced stage of development of the embryos. I have selected a series of ten embryos, representing as many stages of development, the smallest measured three-eighths of an inch in length, the largest seven-eighths of an inch.[2]

In an embryo three-eighths of an inch long the ends of the first and second branchial arches have united in the median line, and a bridge of tissue joins the first and second pair at this place of union; the first fissure is now surrounded with tissue, and is much longer than the second, the difference being greater in embryos one-eighth of an inch longer; the cause of this apparent increase in length is the budding of the superior maxillary process of the first arch; this process is accompanied by a swelling or puffing up of the root of the arch, the boundary between the plateau thus formed, and the neighboring tissue forms a furrow that appears to be a continuation of the first branchial cleft.[3]

This continuation of the cleft has a direction nearly at a right angle with the course of the original fissure, that is, it bounds the end of the first arch while the cleft bounds its lower margin; it gives the embryonic mandible the shape of the adult lower jaw, the original fissure bounding the inferior border of the body, and the continuation that we have just described the posterior border of the ramus; this appearance is very striking in an embryo four-eighths of an inch long.

In one sense this furrow is a part of the first branchial fissure, that is, it borders the first branchial arch. I do not propose to discuss the

[1] On the Structure and Development of the Skull of the Pig. Philosophical Transactions, vol. 164, part 1, 1876.

[2] The embryos were all from the pig; the descriptions apply to specimens hardened in Müller's fluid and alcohol. The measurements were made from the tip of the snout to the tuberosity of the ischium. I would express my thanks to Messrs. John P. Squire & Co., of Boston, for the liberality with which the resources of their large establishment have been placed at my disposal.

[3] It seems to me that Kölliker has cut this furrow in the section which we have referred to (figure 220, page 300, of his Entwickelungsgeschichte); this accounts for the depression in the ectoderm, and at the same time explains the contradiction there noticed.

question, but wish particularly to call attention to it as a secondary formation.

In an embryo four-eighths of inch long the second branchial arch has undergone a marked change in its shape, it appears shorter; instead of its previous form, like that of a tapering finger, it is more pyramidal, the base being quite broad; on the margin of the arch bordering the first cleft there is a little projection into the fissure; on close examination a little circular nodule is seen situated at just this point, the contour of the nodule is not very sharp; it is more easily distinguished with the aid of Brücke's glasses; this projection on the second arch is to be intimately connected with a slight process from the inferior maxillary process of the first arch, or mandible, which is the point that we have compared to the angle of the lower jaw in the adult.

In an embryo five-eighths of an inch long the cleft is wholly closed on the ventral surface of the embryo; the remainder of the cleft is a shallow depression, the posterior wall of which is thicker and more elevated than the anterior. From the former wall there is a small, pointed projection into the shallow fossa; it is the representative of the circular nodule above referred to. A little ridge is also seen making into the depression from the opposite (anterior) wall almost opposite the point of origin of the projection just described; this is the transformed projection from the inferior maxillary process of the first arch, the same that was compared to the angle of the jaw. The ridge bounding this depression sweeps in a curved line, concavity upwards, from the projection first described across the site of the former cleft to the second projection. The depression or fossa runs out superiorly into a little slit, which is the remains of the furrow that apparently formed a continuation of the first cleft. The slit is as shallow as the depression; they are both lined by the common integument. The most careful inspection fails to discover any communication with sub-tegumentary tissue.

In an embryo eleven-sixteenths of an inch long, a little hole about the size that would have resulted from the prick of a pin has formed in the antero-inferior portion of the fossa; the projection that has formed from the nodule on the second arch has increased in size, and is distinctly pointed, but the puffy, thick ridge forms but a blunt point; the slit has become shorter and broader, so that now it resembles the remainder of the depression.

In an embryo three-fourths of an inch long the fossa is nearly round, and its superior and inferior wall make nearly symmetrical curves in passing over to the borders of the pointed projection, spoken of in the description of the embryo eleven-sixteenths of an inch long; this projec-

tion has become thinner, and its apex has commenced a curve which points forward; the meatus is more easily distinguished.

In an embryo seven-eighths of an inch long no mistake is possible; the "pointed projection" is the auricle which points forward over the shallow concha (depression or fossa) in the antero-inferior angle, of which the meatus is seen burrowing into tissue, that at a previous period composed the root of the first branchial arch.

It will be seen that we regard the concha as the only opening remaining from the closure of the first branchial cleft, and this opening is entirely superficial; the ridge forming the auricle is the same evidently as that which Valentin[1] describes as forming the external meatus. It has suggested itself to me that the slit described as extending upward from the depression which forms the concha might explain the little pointed projection on the helix described by Darwin; if it does, this projection has its origin in a defective obliteration of the slit, and it is not a rudiment of the apex of the originally pointed auricle of the lower animals.

The early development of the Eustachian tube can be studied on sections made in a plane anterior to the otic vesicle, and nearly parallel with the general direction of the branchial fissure. The section should incline anteriorly, as it passes downward so as to cut the first arch at an oblique angle. In such a section the commencement of the Eustachian tube is seen as a slight depression in the roof of the pharynx. In an embryo nine-sixteenths of an inch long, a section in the same plane will show that this involution has become deeper, that it points outward and upward, and that it lies in the tissue in which the base of the skull is developed. In an embryo eleven-sixteenths of an inch long the relations are plainer, since the connective tissue surrounding the auditory sac has been transformed into cartilage. At this stage of development, the Eustachian tube is easily distinguished; its course is nearly parallel to that of the cochlea, which as yet is not spiral. A nearly vertical section just anterior to the otic vesicle will pass through meatus and tube so as to show the end of the Eustachian tube overlapping the inner end of the meatus; this relation is still plainer in an embryo a little larger, where the involution forming the meatus is deeper. In an embryo seven-eighths of an inch long, the drum is easily distinguished as a layer of connective tissue bounded below by the meatus which forms its dermoid surface, above by the Eustachian tube which forms its mucous surface. From this description it will be seen that the membrana propria of the drum is a section of embryonic connective tissue. At this stage of development the long process of the hammer is imbedded in it; this description of its formation

[1] Entwickelungsgeschichte des Menschen (Berlin, 1835), p. 216.

also accounts for the position and thickness of the embryonic tympanum.

The hammer and anvil form in the connective tissue above and posterior to the site of the drum; the stapes at first appears to be located in the vestibule rather than in the tympanic cavity; not free in its cavity, however, for it is connected with its wall.[1]

This position of the stapes accounts for the statement generally given by authors, that it forms at a later period than that at which the other ossicles form; it appears later in the tympanic cavity, but I think that its formation begins at about the same time with that of the hammer and anvil. The outer wall of the Eustachian tube lines the drum, and covers in the long process of the hammer; the inner wall shuts the stapes from the tympanic cavity; the body of the hammer and the anvil lie above the end of the tube in the connective tissue from which they are formed; it seems that the formation of the ossicula is directly connected with the formation of the mastoid cells; the growth of the bones is accompanied by an absorption of the connective tissue around them, so that later when, ossification takes place in this tissue, there are only bands composed of a few embryonic cells, and their processes remaining, as a result we have the thin, bony plates, that bound the cavities in the mastoid process.

[1] I do not think that the stapes forms by a process of gemmation from the cartilage of the vestibule, as Mr. Parker states; it seems to me to originate independently, in connective tissue, like the other ossicles.